

pine (as compared to great diversity in California) is attributed to interaction with scolytids. However, ponderosa pine did not occur in Colorado until about 12,000 years ago or within several hundred miles of Colorado as recently as 16,000 years ago. It has occurred in California for a considerably longer period of time. Its recent migration into Colorado alone could have resulted in the lack of genetic diversity observed today. Considerably better evidence of bark beetle limitation of genetic diversity on ponderosa pine must be documented before they can be identified as significant factors in the suggested role.—*Stephen L. Wood, Department of Zoology, Brigham Young University, Provo, Utah 84602.*

**Biological Diversification in the Tropics: Proceedings of the Fifth International Symposium for the Association for Tropical Biology.**—G. T. Prance (ed.). 1982. Columbia University Press, New York. 714 pp. \$60.00.

This large volume champions the thesis that the myriad of moist forest patches (brejos) isolated during the Quaternary in several tropical areas of the world has resulted in a good deal of allopatric divergence and, thus, diversity. The result of such "refugia" are high degrees of endemism. This work is simply one of historical biogeography, which is a province primarily of systematists. Since there are probably more tropical insect species in the world than all other animals, it remains largely for systematic entomologists to grapple with the problem as to how these faunas originated. Although only 5 of the 37 papers in this book deal exclusively with insects (and 4 of the 5 are on Lepidoptera), there is plenty of food for thought on the subject provided by disparate disciplines. Unfortunately, the state-of-the-art on the historical biogeography of the region emphasized in the book, the Neotropics, is not progressive, let alone that of the other regions just casually covered.

Included are a section each on refugia theory and its applications, geology and paleoclimatology, vegetation, insects, vertebrates, primates and anthropology, and the Paleotropics. Redundancy throughout the book makes it much longer than is necessary. The introductions of the majority of papers cite the few early works on the subject and briefly review refugia theory despite the fact that a good introduction is already provided in the first chapter by Haffer. Maps overlap considerably, too, especially of the South American vegetation and climatic zones. Ab'Saber's 1977 map of Pleistocene climates, for instance, is presented twice, each time on a full page. A detailed map section in an appendix would serve for good general reference, although many of the figures in each paper are very informative. Limiting each contribution to four or five pages of original findings would not only have shortened the volume, but would have prevented reiteration of what some five authors (at least to my knowledge) have essentially published elsewhere.

The main accomplishment of the book is detailing endemism among various Neotropical taxa. The botanists, in particular, are very lengthy in their descriptions of floral regions. Some papers, such as those of Steyermark, Andrade-Lima, and Huber on Neotropical plants, are mostly just big lists. Lamas, with the standard zeal that lepidopterists have for geographic variation in wing patterns, lists subspecies of mostly pierids, ithomiine nymphalids, and satyrids endemic to 48 Peruvian sites. Although, as Strong comments, categorizations lead refugia theory to suffer because

they are without precise, falsifiable criteria, such thoroughness is nonetheless the right beginning in understanding the biogeography of a traditionally neglected area.

Some authors do more than just detail endemism and they actually consider floral and faunal relationships. However, as do Grubb (studying African forest mammals), Walker (on the origin of the southeast Asian rain forests), and Magliazza (on linguistic diversity in Amazonian languages), statements of evolutionary relationships are made that rely upon inferences such as those endemic centers of greatest diversity being the center of origin. One could very plausibly argue the opposite, that ancestral regions should be relatively depauperate due to longer exposure to extinction. The obvious shortcoming in most papers is a complete lack of phylogenetic thinking. In this respect, the term refuge—supposedly the theme of the book—is prematurely used, probably because it is such an attractive term to biogeographers. How does one actually recognize a refuge? It is a relatively old area that has provided taxa that have diversified subsequent to its isolation. Pragmatically, criteria and limits should be defined to test, say, the requisite proportion of ancestral species found in a proposed refuge. Such an approach is analogous to what many vicariance biogeographers are doing based upon cladistic reconstructions of a taxon's phylogeny (Patterson, 1981).

The vertebrate contributors are the most advanced in their approaches, which perhaps reflects the status of vertebrate systematics in general. Heyer and Maxson conclude that *Leptodactylus* frogs have diverged prior to the Quaternary in South America, whereas Duellman shows that some refugia have influenced divergence in two *Hyla* species groups. If improved, Heyer and Maxson's approach can be very useful. However, their estimate of *Leptodactylus* divergence time is simply one of the albumins on which the immunological distance matrices were based. With direction given to their phenetic tree, and more loci incorporated, divergence time could then be more accurately compared with the geological date for area divergence. Probably the best conceived and written paper in the book is by Weitzmann and Weitzmann, who (with several other authors) recognize the danger in scenario building based on predetermined notions of occasional dispersal events. They construct a cladogram for each of two small fish genera (*Carnegiella* and *Nannostomus*), but find little congruence between these and refugia proposed on independent grounds. Dispersal to the present-day distributions is then suggested. Several authors, such as Pearson (on birds) and Gentry (on woody angiosperms in Colombia) find that endemism is sometimes a result of specific ecological conditions (due either to extinction in inhospitable areas and/or dispersal to good areas). The preliminary indication is, then, that dispersal has been important in the distribution of many taxa (hardly surprising given the geographic scale of many groups); this should not, however, deter us from adopting a vicariant test as the initial approach (Platnick and Nelson, 1978).

It is interesting that many of the proposed refugia do not overlap among taxa. Exceptional is the very impressive superimposition, shown in Figure 16.36, of the refugia based on ithomiine and heliconiine Nymphalidae subspecies distributions (worked on by K. S. Brown) and the refugia compiled by Brown based on many other data. Oren, at least, proposes that the average size of refugia varies among taxa because of differences in the minimal critical population sizes (i.e., that number needed to sustain a breeding population). This can partly explain a difference in refugia distributions, but the matter as a whole is not attacked.

Dispute between some ecologists and the remainder of the authors provides some

controversy to the topic. Endler antagonizes refugia theory with well constructed arguments. However, his assertions are not well founded that many of the assumptions of refugia theory are unreasonable. For example: Many 'refugiists' do not maintain allopatry is required for divergence, nor that it necessarily results in differentiation. Generally agreed upon is that allopatric speciation is a ubiquitous, but not universal, mode, and that sympatric speciation has certainly enjoyed no resounding support in theory or fact despite the effort to prove otherwise (Futuyma and Mayer, 1980; Jaenike, 1981). Benson, working on *Heliconius* communities, supports Endlers' parapatric model. The argument is that divergence is easily explained by a cline of selection pressures, so much so that vicariance has little influence in distributions. But, Bensons' work deals with a small number of overt racial patterns with simple genetic bases, the appearance of which are demographically mediated. Can one make inferences of faunal origins based on studies of a simple and adaptive trait? This line of argument would also claim that distinct populations of *Biston betularia* have not been affected by any dispersal or vicariant event in England because the appearance of color morphs accord so well with the presence or absence of air pollution.

Erwin and Adis seem to be dealing more with habitat selection in carabids than with the beetles' biogeography. They attempt to reconcile this by stating "habitat vicariance is simply geographic vicariance at a much finer resolution." This seems to suggest that sympatric speciation is the rule rather than exception for creatures of low vagility, such as their arboreal *Agra*. The implication, of course, is that communities can be inherently very unstable assemblages—a very unorthodox view, given the persuasion of this symposium's participants.

Will we ever be able to reconstruct the effects of Quaternary forest fragmentation on tropical diversity? Not unless better distributional and geological data is collected and put into a phylogenetic perspective. At least with our present state of knowledge on endemism, as stressed in the concluding chapters by Myers and by Lovejoy, we can determine the best areas in which to establish natural preserves. For those who feel that the biological diversity of the rapidly depleting tropics will be salvaged and the origins of which are worth studying, I recommend gleaning this book for a few salient references.—*David Grimaldi, Department of Entomology, Cornell University, Ithaca, New York 14853.*

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